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BIONOMICS OF *LASIOGLOSSUM* (*EVYLAEUS*) *MATIANENSE* (BLÜTHGEN) (HYMENOPTERA: HALICTIDAE), THE PREDOMINANT POLLINATING BEE IN ORCHARDS AT HIGH ALTITUDE IN THE GREAT HIMALAYA OF GARHWAL, U.P., INDIA

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Abstract.—The halictine bee, *Lasioglossum* (*Evylaeus*) *matianense* (Blüthgen) is the most abundant bee in early May, pollinating apples soon after snowmelt at Harsil, India (elevation 2600 m), and pollinating *Prunus* sp. at Gangotri, India (elevation 3100 m). It nests in south-facing, sunny banks, where density reaches 2403 nests per m^2 ($\bar{x}$:290 nests per m^2). The nests of this probably solitary species are short, sinuous, nearly horizontal burrows, ending in 1 or 2 cells at a mean depth of 6.2 cm. This bee thermoregulates its nests by placing them in relatively cool, moist soil among grass roots near the tops of the banks.

Key Words: Himalaya, pollination, apple, *Prunus*, bee, nests, thermoregulation

Worldwide, there are about 2,000 species of halictine bees, popularly called 'sweat bees' because some lick salty sweat. They are important pollinators of crops and wild plants in all terrestrial habitats, including Arctic tundra, the world's highest mountains, wettest rainforests, driest deserts, vast prairies, temperate forests, and urban gardens. Because most species are small, dark, and inconspicuous, and nest underground, people often overlook them, even when they are very abundant in habitats. They are also difficult to identify taxonomically. Halictine bees, including *Evylaeus*, are of great interest for the study of sociobiology and evolution, because they have such a diversity of social behavior, ranging from strictly solitary species to communal, semisocial, and eusocial (*sensu* Batra 1966) bees that share nests (see Packer and Knerer 1985 for a review). Some species may be eusocial in a favorable habitat with a long growing season, but live a solitary life where the growing season is too short to permit the development of social colonies, for example, *L.* (*Evylaeus*) *calceatum* (Scopoli) (Sakagami and Munakata 1972).

The subgenus *Evylaeus* of *Lasioglossum* is most abundant and diverse in cold climates of North America and Eurasia. Two species, *L.* (*E.*) *rufitarse* (Zetterstedt) and *L.* (*E.*) *borealis* Svensson, Ebmer, Sakagami, are Holarctic (Sakagami and Toda 1986). *Evylaeus* is divided into two groups, those in which the females have a carina on the posterior edge of the propodeum (Svensson et al. 1977), and those without a carina. Carinate species often construct their nests so that the subterranean brood cells are arranged to form delicate earthen combs that are surrounded by airfilled cavities (Batra 1990). In general, nests of carinaless species lack combs (based on a sample of fewer than 20 species). According to A. W. Ebmer (in litt.), *L.* (*Evylaeus*) *matianense* (Blüthgen, 1926) belongs to the holarctic *L.*

(*E.*) *nitidiusculum* taxonomic species-group.

From March 5 to May 8, 1995, I undertook a survey of bees that pollinate rosaceous fruit crops in the Garhwal Himalaya, U.P., India (Batra in press). The Shivalik range and Lesser Himalaya were surveyed at several locations (77°30′ to 79°00′E; 30°15′ to 30°30′N), at altitudes from 579 to 3100 m above M.S.L. during March and April. Beginning on May 1, I studied the pollinators of apples growing at and near Harsil (elevation 2600 m; 78°45′E, 31°02′N) and *Prunus* sp. at Gangotri (elevation 3100 m; 78°57′E, 31°00′N). This area is in the subalpine zone of the Great Himalaya Range (Mani 1962; Mani 1978), about 20 km south of the Tibet (China) border, in a deep valley on the upper Bhagirathi Ganga River, surrounded by snow-capped peaks of over 6000 m elevation. Apples are grown on terraced slopes to 3100 m elevation. Timberline is at about 3600 m. Mornings were clear, but strong southerly orographic updrafts brought haze, clouds and chilly precipitation after noon, and cold, katabatic drafts blew down from the glaciers to the north at night. The pollinating bees on early-bloom apples and full-bloom pears at first included no honey bees. Almost all of the bees were halictines, especially *L.* (*E.*) *matianense*. Various Diptera were abundant on the apple flowers. No *Apis cerana* F. live at, or north of, the apple-growing district of Sukhi (elevation 2487 m) where, according to local growers, beekeeping is not practiced. *Apis laboriosa* Sm. foragers suddenly appeared on apple blossoms at Harsil on May 5. They were some 600 km west of the previously known range of this seasonally migrating giant honey bee in Nepal (for behavioral details, see Batra 1996).

Although some 9000 species of seed plants grow in the 1450 km² area of the western Himalaya that is above 1200 m elevation (Polunin and Stainton 1984), and some 4000 species are endemic to the Himalaya (Mani 1978), very little is known about their pollinators, most of which may be endemic, as are other Himalayan insects (Mani 1962). Due to its remoteness and difficulty of access, the bees of the Great Himalaya Range are practically unknown. No work on the pollination of the temperate crops that are grown in these enormous, extensive, and rugged mountains has been conducted. This is significant, because this region is adjacent to the centers of origin for several important crops, thus, efficient coevolved pollinators of these crops should occur there. Previous work on crop pollination in the Himalaya has been conducted in the Lesser Himalaya, which are influenced by the monsoon and have a more moderate climate (Batra in press).

The Harsil area is of particular ecological interest because it lies just north of the crestline of the Great Himalaya Range. Harsil and Gangotri are in the rain shadow of Srikanta (6132 m elevation), Jaonli (6632 m) and Phating Pithwara (6904 m), which partially block the southeast monsoon. *Artemisia* and other xerophytes that are characteristic of Middle Asia (Mani 1978) grow there. The river valley and its orchards are surrounded by extensive glaciated areas. Apple orchards were first planted beside the river at Harsil about 75 years ago, and some of the original trees are still living there, according to local growers. Apples and other fruit trees were subsequently planted extensively on terraces where the native *deodar* cedars were cleared, from Sukhi to the south (2500 m elevation) and at several locations along the river, to the east and upstream of Harsil, as far as Gangotri (elevation 3100 m). These may be among the world's higher orchards (Fig. 2). Apple varieties include c.v. 'Delicious', c.v. 'Bijou' and a wild-type, seedy, 'Kashmiri' apple. Other fruits grown at sheltered sites along the river in the area include pear, plum, quince, *chulu* apricot, and almonds.

Pollination

I collected apple pollinators on May 1 and from May 5 to 7 at Harsil, by sweeping

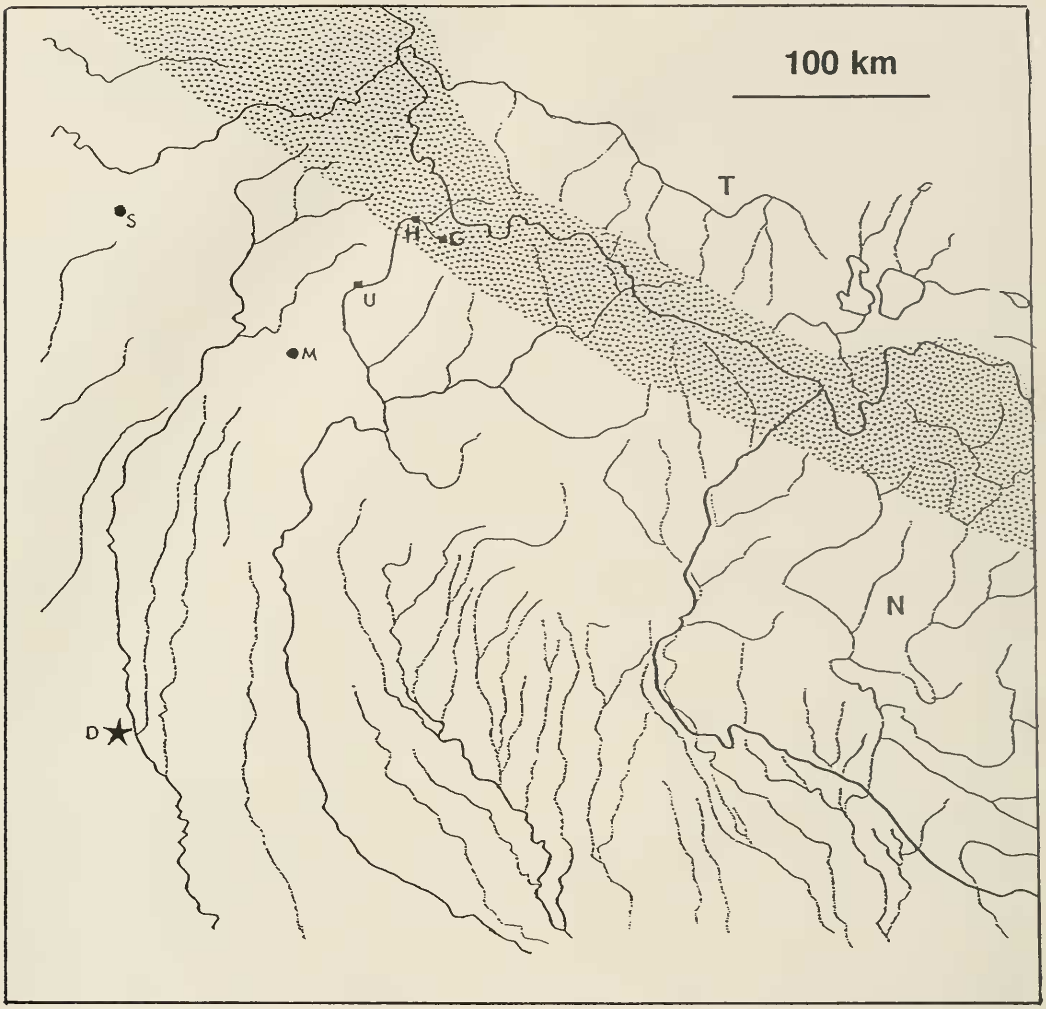

Fig. 1. Location where *L.* (*E.*) *matianense* was collected in Garhwal: H, Harsil; G, Gangotri. The stippled area represents the Great Himalaya Range (Himadri), where many peaks are over 6,000 m and valleys are over 2000 m. Other locations are: T, Tibet; N, Nepal; U, Uttarkashi; D, Delhi. Shimla (S) and Mussoorie (M) are 'hill stations' on the crests of ridges at 2206 m and 2006 m respectively, in the Lesser Himalaya (Himanchal). Between Himanchal and Himadri are subtropical valleys, as low as 500 m in elevation.

the canopy with a long-handled insect net. Although sunrise occurred at 6:30 local time, due to the chilly nights, bees did not begin to fly until 9:00, and maximum foraging activity was between 10:00 and 13:00. In the early afternoon, strong southerly winds and cloudiness developed daily. The bees were very sensitive to any dimming of the brilliant sunshine, and they left the orchard before rain, hail, and snow fell.

The most abundant pollinating bee on apple bloom at Harsil was *L.* (*E.*) *matianense*. On May 1, 93% (98 of 106) of the bees that were collected were this species. At another site near Harsil on May 6, 75% (49 of 65 bees) on apples were *L.* (*E.*) *matianense*. I also collected pollinators on *Prunus* sp. (? *P. mira*) growing near melting snowbanks on May 3 and 4 at Gangotri (apples were not yet in bloom there). At this location, also, *L. matianense* was the predominant bee. For comparison, at

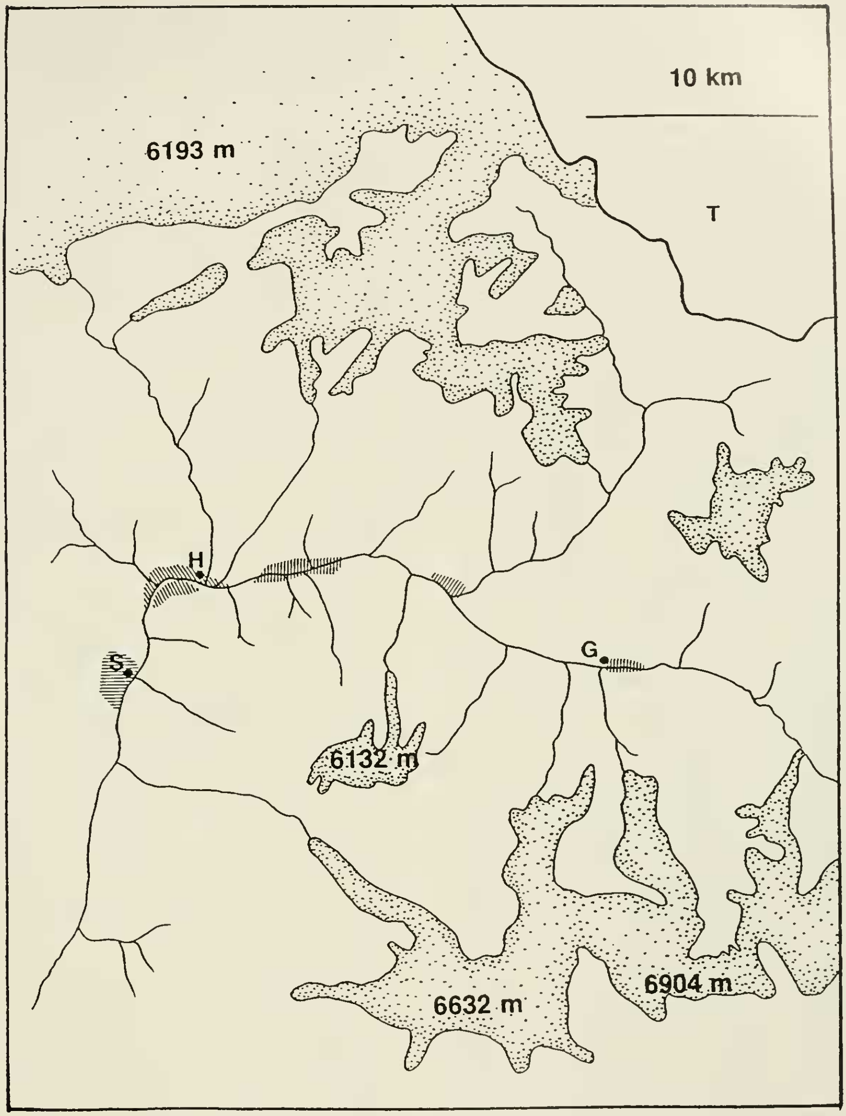

Fig. 2. Map of the Harsil area, showing surrounding high peaks (numbers indicate elevation in meters), glaciated areas (stippled), and locations of the orchards (hatched areas). S = Sukhi; H = Harsil; G = Gangotri; T = Tibet.

Dhanaulti (2200 m elevation) in the Lesser Himalaya, *Apis cerana* were by far the most abundant pollinators of apples in mid-April; beekeeping being widely practiced there. Halictine bees, especially both sexes of *L.* (*E.*) *marginatum* Brullé, were second in abundance (at about 10% of the total). The predominance of halictines at high elevations, and the scarcity of *Andrena*, *Osmia*, and *Bombus*, both in numbers of individuals and in diversity of species, were unexpected findings. These three genera (especially *Andrena* spp.) are the most important native, unmanaged apple pollinators in North America and Europe (Boyle and Philogène 1983; Boyle-

Makowski 1987; Scott-Dupree and Winston 1987, and references therein).

Aggregation and Thermoregulation

A large aggregation of the nests of *L.* (*E.*) *matianense* was discovered on May 7, in a steep, sunny, south-facing slope, about 100 m above the orchard near Wilson Cottage at Harsil. Foraging females were returning with large loads of apple pollen. This slope was an overgrazed pasture, where most of the original *deodar* cedars had been removed. Scattered large trees provided patches of shade. Several trails had been cut into the slope by grazing yaks, mules, and goats, and the bees' nests were in the ca. 0.5 to 1.0 m-high bank of soil that had been exposed on the upslope sides of these livestock trails. The underlying soil was glacial till, a mixture of fine, micaceous silt and sand, mixed with pebbles, cobbles, and flat, gleaming, micaceous rocks. Above it was 20–30 cm layer of moist loam, filled with the rootlets of short grasses and forbs, such as *Taraxacum* and *Fragaria*, that were just beginning their spring growth. This area was probably glaciated within the past 10,000 years. The Bhagirathi Ganga River emerges from a retreating glacier near Gangotri at about 4000 m elevation. Next to the zigzag livestock trails, *L.* (*E.*) *matianense* nests formed patches of dense aggregations where the south-southeast aspect and insolation appeared to be favorable. Counts of all nest entrances in 31 meter-square sections were made at 5 locations within a 100 m^2 area, along 4 of the trails. Total nests per m^2 included samples with mostly soil, and samples that contained large, obstructing rocks and roots, which were less favorable for nesting. Results are as follows:

Site 1 (7 m^2 samples): 20 (rocky) to 348 nests per m^2; $\bar{x}$ = 165 nests per m^2.
Site 2 (6 m^2 samples): 10 (roots) to 545 nests per m^2; $\bar{x}$ = 115 nests per m^2.
Site 3 (12 m^2 samples): 50 to 2403 nests per m^2; $\bar{x}$ = 376 nests per m^2.
Site 4 (5 m^2 samples): 15 (rocky) to 369 nests per m^2; $\bar{x}$ = 182 nests per m^2.
Site 5 (1 m^2 sample): 130 nests.

The mean for all 5 sites was 290 nests per m^2; 7303 nest entrances were counted within the 31 m^2 total area surveyed. Because similarly suitable habitat extended for an estimated 300 m along the livestock trails on the slope above the orchard, as many as 87,000 nests of *L.* (*E.*) *matianense* may have been present.

The Himalaya are notable for extreme variability of microclimates, the result of their high elevation, rugged terrain, continentality, and relatively low latitude. A combination of diurnal insolation and nocturnal radiation, atmospheric aridity, cold, low oxygen pressure, rapid desiccation, strong winds, and extreme daily temperature fluctuations affects all life. Small, microclimatic differences in aspect, light and shade may change the length of the growing season and time of erop maturity at a location by up to 3 weeks (Whiteman 1985). At the elevation of Harsil, the frost-free growing season is about 24 weeks (Mani 1978). In the Great Himalaya, the atmospheric mean temperature increases rapidly from March to June, but then it stabilizes by July, due to monsoon cloud cover, before declining after August (Mani 1978). *Lasioglossum* (*E.*) *matianense* has exploited the brief period of intense insolation and warmth that exists in May and June, when it makes and provisions its nests and its brood develops. It has also exploited the phenomenon that south-facing slopes receive twice as much solar radiation as north-facing slopes (Whiteman 1985), by nesting in south-facing slopes. In North America, the vernal bee *L. (Evylaeus) comagenensis* (Knerer and Atwood) similarly nests where it maximizes insolation (Batra 1990a), as do *Andrena alleghaniensis* Viereck (Batra 1990b) and *A. fenningeri* Viereck (Batra, in litt.). In Japan, *L.* (*Evylaeus) duplex* (Dalla Torre) selects nest sites that receive direct morning sunshine (Sakagami and Hayashida 1961).

The nests of *L.* (*E.*) *matianense* were not randomly distributed in the banks next to the livestock trails. The great majority of nests were in the topmost layer of soil at all of the 31 sites examined. Nests were made in a 10–15 cm thick zone of dark, loamy, moist soil, among the tough, fibrous rootlets of the short turf grasses and forbs. The entrances to many nests were hidden, and partly shaded by an overhanging thatch of grass blades and dangling rootlets (Fig. 3). At site 3, where nests were the densest (2403 per m^2), nest entrances were as close as 2 mm. This made orientation difficult for returning foragers, which hovered, zigzagging in front of the bank, before finding their nests. About 150 flying, humming, bees per m^2 were visible at a glance. This is one of the higher nest densities among bees. Another solitary species, *L.* (*Evylaeus*) sp. nr. *fulvicorne* (Kirby) nests in aggregations that reach 101 nests per m^2 ($\bar{x}$ = 54 per m^2; Maeta 1966).

In order to study the reason for the limited dispersal of the nests of *L.* (*E.*) *matianense*, two calibrated, bimetallic, dial probe thermometers were inserted at 2 locations into the soil at site 3 and kept there all day. One thermometer was inserted to depths of 5, then 15 cm, into the moist, loamy rootlet zone where the maximum nests had been made. The other thermometer was inserted near the first, at 5, then 15 cm, in a drier, sandy area about 30 cm below the first, where there were no nests. Temperatures were recorded periodically at 5 and 15 cm in the nest zone and at the same times in the nestless zone. The moist, loamy soil that was selected by the bees for nesting maintained a more constant and lower daily temperature than the sandy soil that was avoided by the bees (Fig. 4). Evidently, the insulating thatch of grass and the moisture retained by the rootlets buffered the nests and brood cells (mean depth, 6.2 cm) from daily temperature extremes and desiccation.

Nest Architecture

Fourteen complete, open nests with brood cells and 23 miscellaneous cells of *L.* (*E.*) *matianense* were excavated (Fig. 3). The circular nest entrances were 2.5 to 3.0 mm in diameter, and were somewhat irregular, without any noticeable modifications made by their inhabitants. The main tunnels were sinuous, 4.0–4.5 mm in diameter, and 2.5 to 11.0 ($\bar{x}$ = 6.2) cm deep, ending in a cell. Eleven nests terminated at one cell, and 3 nests had 2 cells each. The nest tunnels were intertwined among each other and among rootlets and stones. The friable, fine, loose soil and rootlets made it difficult to trace individual tunnels.

The contents of undamaged brood cells varied. Five cells were new, open, and unprovisioned, smelling of the characteristically tangy Dufour's gland secretion, which is used by the bees to waterproof the interior of cells. Marks made by pygidial plates could be seen in their shiny, smooth interiors. The slightly milky, transparent secreted cell linings penetrated the surrounding soil, which contained flat mica particles that formed a terrazzo-like pattern in cells. The cells were of the usual halictine shape (Fig. 3). Five cells were open, containing small, incomplete balls of moist, medium-yellow apple pollen, with a dusting of loose, dry pollen. Ten cells were sealed with a plug of loose soil. Each of these contained a moist, medium-yellow flattened spheroid of pollen with a groove on top containing an arched, white 2.0 mm-long egg. These pollen balls were 3.5–4.0 mm in diameter and 2.0–2.5 mm high. They contained 95% apple pollen (n = 5). Brood cells were 7.5–9.0 mm long, and 4.0–4.5 mm in maximum width, with a 2.0–2.5 mm neck. No cells contained larvae, pupae, or adults. The distal ends of about 80% of cells extended into the bank, but the ends of some cells were directed toward the front of the bank, when burrowing bees had encountered rocks. Some cells were built

Fig. 3. Nests of *L.* (*E.*) *matianense* among the fibrous rootlets of grasses in the loamy, moist, upper 10–15 cm of a sunlit bank next to a livestock trail.

against rocks, separated from them by 1 mm of soil.

There was no evidence of social behavior, which is unlikely to develop, due to the brief growing season. One nest contained a female cleptoparasitic halictine, *Sphecodes* sp.; others were empty or contained a single *L.* (*E.*) *matianense* female. No male *L.* (*E.*) *matianense* was collected at the nest site or in the orchards. There were few traces of

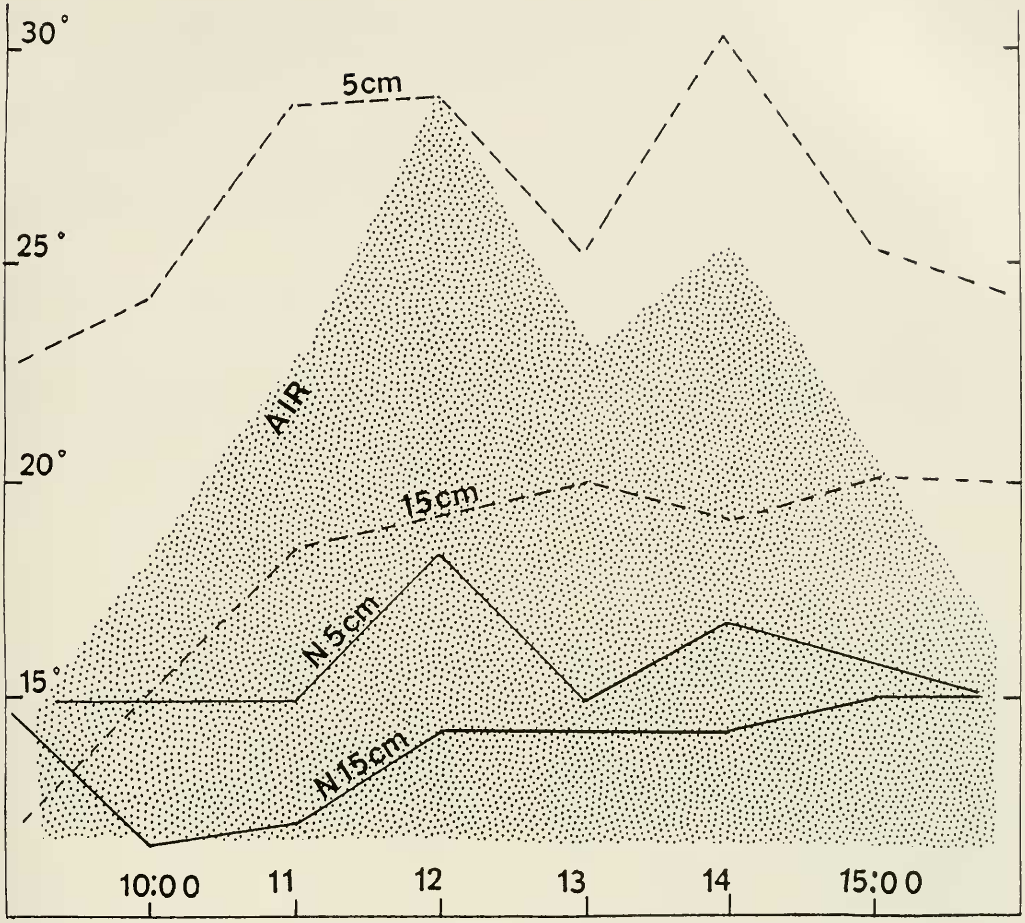

Fig. 4. Thermoregulation may be accomplished by the placement of nests. The moist, loamy soil in the upper 20 cm of the bank among the rootlets where *L.* (*E.*) *matianense* nests (N) stays cooler, and temperatures there, at 5 cm and 15 cm, fluctuate less, than in the lower, drier, and sandier portion where the bees did not nest (dashed lines). Diurnal air (stippled area) and soil (lines) temperatures were recorded on May 7.

abandoned cells from previous years' nesting. Frass from one such cell contained apple pollen exine.

Conclusion

The simple, combless nests of *L.* (*E.*) *matianense* resemble the nests of the Holarctic, solitary, boreal species *L.* (*E.*) *borealis* (Svensson et al. 1977; Sakagami and Toda 1986). Other similarly combless, solitary, boreal species are *L.* (*E.*) *sakagamii* which ranges from northern Japan to Manchuria (Sakagami et al. 1982), and *L.* (*E.*) *allodalum* Ebmer et Sakagami, from northern Japan (Sakagami et al. 1985). The other solitary, Palearctic species of *Evylaeus* make earthen combs of cells; for example, *L.* (*E.*) *nupricola* Sakagami, a boreo-alpine, ice-age relic in northern Japan (Sakagami 1988), and *L.* (*E.*) *calceatum*, which is solitary at high, cold elevations, but is eusocial in more temperate zones (Sakagami and Munakata 1972).

Himalayan apple growers could improve pollination by providing habitat for nests of *L.* (*E.*) *matianense* near their orchards. The trees should be grown on, or near, south-facing, sunny, turf-covered slopes, where vertical cuts have been made, to expose bare soil banks for nesting bees.

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